COMPARATIVE MORPHOLOGICAL STUDIES IN DILLENIACEAE, II. THE POLLEN

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In a previous paper (Dickison, 1967) it was indicated that since a comprehensive comparative morphological investigation of the Dilleniaceae had never been undertaken, such a study might prove very rewarding in the attempt to discover the phylogenetic relationships of this interesting tropical family. The lack of prior morphological work on the Dilleniaceae is particularly evident in the area of pollen morphology. This can be attributed, in part, to the comparatively recent application of palynological data in solving taxonomic problems.

Erdtman (1952) gives a limited description of three genera and seven species of Dilleniaceae. From this treatment he concluded that "pollen morphology seems to support the assumption that Dilleniaceae should be related to Polycarpicae."

In the only other significant reference to dilleniaceous pollen, Barth (1962) described in detail the pollen of four species belonging to the genera *Davilla*, *Doliocarpus*, and *Tetracera*. It was this worker's opinion that the family represented a parallel group to the Magnoliaceae from which it had previously been thought to be derived.

The present study was carried out in order to provide evidence to be evaluated from all organs and parts of the plants in an effort to determine the affinities of the Dilleniaceae.

MATERIALS AND METHODS

Pollen of all ten dilleniaceous genera was examined. The source of material was basically threefold: (1) liquid preserved (FAA) or dried specimens sent to the author; (2) exchange slides from the Harvard Pollen Collections (HPC), Pan American Oil Co., and the Rancho Santa Ana Botanic Garden (RSA) and (3) herbarium specimens obtained from the University of California, Berkeley (UC); Missouri Botanical Garden, St. Louis (MO); New York Botanical Garden (NY); and the United States National Herbarium, Washington (US) to whom I am especially grateful for providing material of the rare genus *Acrotrema*.

Pollen was prepared by the standard acetolysis method outlined by Erdtman (1960). Material was subsequently mounted in glycerine jelly. This procedure generally left grains with a darkened exine which made staining unnecessary. In a few cases, however, a basic fuchsin dye was employed with good results. Difficulty was encountered in removing the

protoplasm from grains preserved in formalin-acetic acid-alcohol (FAA). In some samples there was a tendency for the protoplasm to become plasmolyzed into a sphere which was never successfully removed.

The fact that pollen prepared by the acetolysis method is larger than pollen prepared by other means (e.g., lactic acid, KOH, etc.) is now well established (see Canright, 1953). Carlquist (1961) is of the opinion that not enough emphasis has been placed on the fact that pollen morphology is highly influenced by methods of preparation. In a recent discussion of this problem, Whitehead (1965) also stresses the need for a uniform mounting medium; however, he does not recommend glycerine jelly.

Despite opposition to the acetolysis-glycerine jelly method, the ease of preparation, wide application in palynological research, and generally excellent results obtained, justify its employment in comparative morphological investigations.

With the above discussion in mind, in addition to personal experience, I concur with Canright (1963) that pollen size and shape are the most unreliable of diagnostic features.

In order to minimize usage of complex and confusing terminology, the suggestions of Faegri and Iversen (1964) are followed. All measurements and descriptions were made under oil immersion ($\times$ 1000). Size dimensions were determined by measuring at least twenty grains from each sample. No effort was made to treat the numerical data statistically. The dimensions are, accordingly, only intended to indicate relative size ranges. Pollen descriptions of putatively related families were obtained for the most part from Erdtman (1952).

OBSERVATIONS

1. Dillenia L. (Figs. 1–3)

The pollen grains of *Dillenia* are the most variable in the family with respect to both sculpturing and aperture type. SHAPE: Oblate, oblate-spheroidal or spheroidal; circular to semiangular in polar view. SIZE: [1] Avg. dimensions for all species examined, ca. 21.7μ (P) $\times$ 24.9μ (E). The largest grains were recorded for *D. reifferscheidia* (25.2μ $\times$ 32.2μ). STRUCTURE: Tectate or rarely semitectate. Endexine generally equal in thickness to ektexine. SCULPTURE: Scabrate to reticulate-rugulate to most frequently reticulate. APERTURE: Triporate in *D. indica* and *D. philippinensis*; tricolpate in *D. turbinata, D. reifferscheidia, D. alata, D. excelsa,* and *D. papuana*; tricolpate with rare or occasional tetracolpate grains in *D. suffruticosa, D. ovata,* and *D. luzoniensis.* Triporate grains have elongate pores and are provided with a well-defined annulus. Tricolpate and tetracolpate forms have granular furrows which may or may not have opercular membranes and margo. Furrows extend about three-fourths the length of the polar axis.

[1] P refers to dimension of polar axis, E the length of equatorial axis.

2. **Hibbertia** Andr. (Figs. 4–6, 21)

SHAPE: Oblate to spheroidal to prolate spheroidal; circular to sub-angular in polar view. SIZE: The smallest grains were recorded for *H. salicifolia* ($18.9\mu \times 17\mu$) and the largest for *H. stricta* ($34\mu \times 32.2\mu$). Avg. size for all species examined, ca. 25.2μ (P) $\times$ 27μ (E). STRUCTURE: Tectate; endexine equal in thickness to ektexine. SCULPTURE: Foveolate (e.g., *H. stellaris* and *H. salicifolia*) to most frequently reticulate. APERTURE: Tricolpate, furrows granular, often provided with opercular membrane and margo. Furrows either quite distinct and wide (10μ), in which case they extend the entire length of polar axis (e.g., *H. cuneiformis* and *H. tetrandra*), or else, not well defined and extending about two-thirds the length of polar axis (e.g., *H. hexandra*). Erdtman (1952) describes *H. acicularis* as tricolporate, a condition which was not observed in any of the samples examined in this study.

3. **Pachynema** R. Br. (Fig. 9)

SHAPE: Spheroidal to prolate spheroidal; circular in polar view. SIZE: ca. 16.4μ (P) $\times$ 16.1μ (E). STRUCTURE: Tectate or semitectate; endexine equal in thickness to ektexine. SCULPTURE: Foveolate to reticulate. APERTURE: Tricolpate, furrows granular and not well defined, extending entire length of polar axis.

4. **Schumacheria** Vahl (Fig. 8)

SHAPE: Oblate spheroidal; mostly rectangular to spheroidal in polar view. SIZE: ca. 15μ (P) $\times$ 16.5μ (E). STRUCTURE: Tectate; endexine equal in thickness to ektexine. APERTURE: Tetracolpate, rarely tricolpate; furrows poorly defined and extending about one-third the length of polar axis. Slight thickening of ektexine at margins of furrows.

5. **Acrotrema** Jack (Fig. 7)

SHAPE: Oblate spheroidal; semiangular in polar view. SIZE: ca. 18μ (P) $\times$ 21μ (E). STRUCTURE: Tectate; endexine equal in thickness to ektexine. SCULPTURE: Finely reticulate. APERTURE: Tricolpate, furrows granular and provided with opercular membranes.

6. **Didesmandra** Stapf (Fig. 10)

SHAPE: Oblate spheroidal; mostly rectangular to subangular in polar view. SIZE: ca. 25.7μ (P) $\times$ 28μ (E). STRUCTURE: Tectate; endexine equal in thickness to ektexine. SCULPTURE: Reticulate. APERTURE: Tetracolpate, occasionally tricolpate; furrows extend about one-third the length of polar axis.

7. **Curatella** Loefl. (Figs. 16, 17)

SHAPE: Spheroidal to prolate spheroidal to occasionally prolate; circular in polar view. SIZE: ca. 23μ (P) $\times$ 20μ (E). STRUCTURE: Tectate;
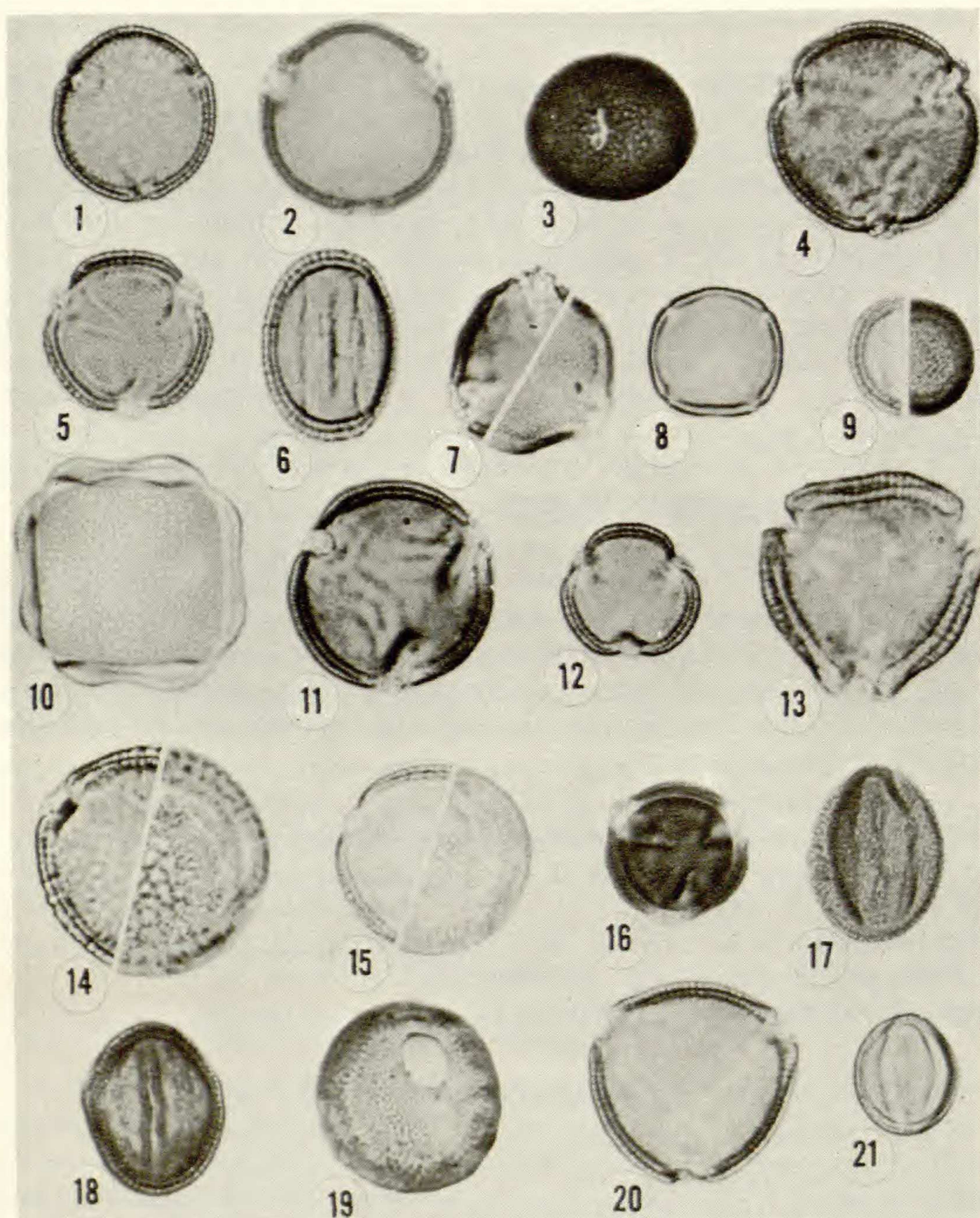
FIGS. 1–21. Dilleniaceous pollen (all ca. × 1000). 1, *Dillenia suffruticosa* (cult. SING *s.n.*), polar view showing tectate structure. 2, *Dillenia indica* (cult. BRI *s.n.*), polar view. 3, *the same*, equatorial view of elongate pore. 4, *Hibbertia stricta* (HPC 2981), polar view depicting tectate structure and prominent opercular membranes. 5, *Hibbertia scandens* (cult. K *s.n.*), polar view. 6, *the same*, equatorial view. 7, *Acrotrema bullatum* (US 1576874), polar view in two focal levels, note granular membranes. 8, *Schumacheria castaneifolia* (Abey-wickrama *s.n.*), polar view of tetracolpate grain. 9, *Pachynema dilatatum* (NT 6129), polar view in two focal levels showing reticulate exine. 10, *Didesmandra aspera* (Burtt 2540), polar view showing reticulate exine. 11, *Tetracera fagifolia* (HPC 6270), polar view showing tectate structure. 12, *Tetracera asiatica* (HPC 1835), polar view, note opercular membranes. 13, *Davilla rugosa* (HPC 2953), polar view of tricolporate grain. 14, *Davilla kunthii* (UC 963504), polar view in two focal levels showing nature of reticulum. 15, *Doliocarpus dentatus*

endexine equal in thickness to ektexine. SCULPTURE: Finely reticulate. APERTURE: Tricolpate, furrows provided with opercular membranes and margo, extending entire length of polar axis. A limited number of grains observed were questionably tricolporate but the occurrence of this feature could never be satisfactorily proven.

8. Davilla Vandelli (FIGS. 13, 14)

SHAPE: Spheroidal to subspheroidal; circular to semiangular in polar view. SIZE: Avg. size for all species examined, 26.2μ (P) × 25μ (E). STRUCTURE: Tectate; endexine equal in thickness to ektexine. SCULPTURE: Reticulate to coarsely reticulate (e.g., *D. kunthii*). APERTURE: tricolporate; furrows provided with an operculum. Pores granular, spheroidal to slightly elongate. The pollen of *D. rugosa* has previously been described and diagrammed as tetraporate (Barth, 1962). My observations show that this species possesses three well-defined furrows and is, therefore, tricolporate.

9. Doliocarpus Roland. (FIGS. 15, 19, 20)

SHAPE: Spheroidal to prolate spheroidal to prolate; circular to semiangular in polar view. SIZE: Avg. size for all species examined, 24μ (P) × 20.6μ (E). STRUCTURE: Tectate; endexine equal in thickness to ektexine. SCULPTURE: Finely reticulate to reticulate. APERTURE: Tricolporate, furrows may or may not be provided with a margo extending three-fourths the length of polar axis. Pores indistinct due to opercular membrane, generally circular in outline.

10. Tetracera L. (FIGS. 11, 12, 18)

SHAPE: Spheroidal, prolate spheroidal or prolate; circular in polar view. SIZE: Avg. pollen size in this genus can be correlated with geographical distribution. The largest grains occur in the New World species (ca. 26.5μ (P) × 22.7μ (E)), the smallest in the Indo-Malayan species (diam. ca. 18.5μ), whereas African forms are intermediate (ca. 22.8μ (P) × 20.4μ (E)). STRUCTURE: Tectate; endexine equal in thickness to ektexine. SCULPTURE: Finely reticulate to reticulate. APERTURE: Mostly tricolporate, tricolpate in *T. alnifolia*; furrows and pores granular, provided with opercular membranes, pores generally circular in outline.

SUMMARY OF POLLEN MORPHOLOGY OF DILLENIACEAE

The pollen grains of the Dilleniaceae vary in shape from oblate to spheroidal to prolate. The smallest grains were recorded for *Schumacheria castaneifolia* (15μ × 16.5μ), while the largest occurred in *Hibbertia*

(HPC *2962*), polar view in two focal levels. 16, *Curatella americana* (*Irwin 5470*), polar view. 17, *the same*, equatorial view. 18, *Tetracera alnifolia* (MO *1598748*), equatorial view of tricolpate grain with prominent margo. 19, *Doliocarpus major* (HPC *6272*), equatorial view showing well defined pore in granular furrow. 20, *the same*, polar view. 21, *Hibbertia stellaris* (HPC *1837*), equatorial view showing elongate furrows.

stricta (34μ × 32.2μ). The median size for all genera examined was ca. 22.4μ (P) × 21.7μ (E). Pollen was exclusively tectate or rarely semitectate, with no significant difference in thickness between endexine and ektexine. Sculpturing is predominantly reticulate or a modification of reticulate. Four basic aperture types can be recognized as existing within the family: triporate, tricolporate, tricolpate and tetracolpate. Segregation of tricolpate and tetracolpate genera is not always strict because of species in which both conditions exist. Likewise, separation of tricolpate and tricolporate aperture types is often difficult owing to the presence of granular opercular membranes.

DISCUSSION

Dilleniaceous pollen is characterized by a relatively large number of morphological types. Unfortunately, the family cannot be successfully divided into tribes or subfamilies on the basis of pollen morphology. This is due to the variation within and overlap between genera in diagnostic features.

Briefly stated, morphologists now generally agree that the monosulcate pollen grain, with a distal solitary furrow, represents the primitive condition in dicotyledons (Eames, 1961, p. 161). Pollen of this nature is found only in dicot families which are known to have general ranalian affinities. In contrast, the more common tricolpate dicotyledonous grain has three meridional furrows or modifications thereof. It has long been difficult for botanists to explain the derivation of tricolpate pollen from the monosulcate type. Wodehouse (1936) suggested a derivation from a spore bearing a triradiate crest. Such an origin was originally supported by the morphology of certain ranalian pollen grains (*Schisandra*). Wilson (1963) has offered an alternative explanation by theorizing that the tricolpate grain may have resulted from a trichotomosulcate condition (as found in some Canellaceae) by loss of furrow contact at the distal pole. Meeuse (1965) believes that the distal extension of the furrows in some tricolpate dilleniaceous pollen supports the latter hypothesis. Since trichotomosulcate pollen was not observed in any Dilleniaceae, such presumptions can only be looked upon with skepticism.

There are at present no widely accepted trends for pollen specialization above the tricolpate level, although some have been suggested for individual families (e.g., Dahl, 1952). Therefore, it is difficult to assess phylogenetic relationships within the Dilleniaceae on this basis.

If it is assumed, however, that the tricolpate grains with very extended, wide furrows (as illustrated in the woody hibbertias) are the most primitive pollen types in the family, phylogenetic specializations could be hypothesized. Advancement in one line could possibly have led to the tricolporate grain, while in another direction a continuing reduction of furrow length would arrive at the triporate condition. It might also be suggested that there was a trend for the addition of an extra furrow which culminated in the tetracolpate forms. Species with both tricolpate and tetracolpate pollen stand as intermediate in this advancement.

Admittedly, there is no sound basis for this sequence. Since it would be dangerous to correlate pollen morphology with data derived from other parts of the plant, it should be emphasized that the data obtained from palynology alone does not provide evidence for any trends of pollen specialization in the Dilleniaceae.

Few similarities can be observed between the pollen of the Dilleniaceae and that of the ranalian complex of families. This is opposed to the opinion of Erdtman (1952) who advanced such an alliance on the basis of palynological evidence. Pollen grains of the Magnoliaceae and Canellaceae are monosulcate or modifications of monosulcate types (trichotomosulcate and dichotomosulcate). Pollen of the Calycanthaceae varies from monosulcate to zonaperturate (belted) to bicolpate to infrequently tricolpate (Bailey, 1960) and is reticulated or baculate. Winteraceae pollen is shed in tetrahedral tetrads whereas that of Annonaceae is nonaperturate, monosulcate, or occasionally shed in coherent tetrads. A survey of other ranalian pollen forms reveals not a single family which closely approximates the Dilleniaceae in aperture type, size, and/or sculpturing.

Within the Parietales (sensu Engler & Prantl, 1893), the eurypalynous Sterculiaceae and the Eucryphiaceae with bicolpate (syncolpate), very small grains offer no foundation for considering these families closely allied to the Dilleniaceae.

The relationship of the Dilleniaceae to the Brunelliaceae, Ochnaceae, Connaraceae, and Theaceae is not as conclusive. These families all resemble the Dilleniaceae in pollen morphology in having either tri (tetra) colpate or tricolporate pollen, although unusual bilateral, subisopolar, tetracolpate grains are encountered in one subfamily of Connaraceae. Pollen exines in these families are psilate to reticulate with the exception of the baculate Brunelliaceae. Size dimensions are also in approximate agreement.

Information gathered from pollen morphology in determining the affinities of *Actinidia* and *Saurauia* is likewise inconclusive. *Actinidia* is characterized by tricolporate pollen which has an indistinct psilate exine. *Saurauia* pollen is quite variable as evidenced by the occurrence of tricolporate, triporate, and tetra (col) porate grains, as well as coherent tetrahedral tetrads. Exines are all predominantly psilate.

The pollen of *Crossosoma* is tricolporate or bicolporate, prolate, and the grains have reticulated exines. *Paeonia* pollen is tricolporate, with smooth furrows but pores covered by granular membranes, prolate spheroidal and reticulated. The size of the pollen in these two genera closely approximates that of the pollen of Dilleniaceae.

In conclusion, the data presented from pollen morphology does not provide a definite clue to the phylogenetic relationships of the Dilleniaceae. Nevertheless, I believe the comparatively specialized tricolpate, tricolporate, triporate, tetracolpate, and reticulated pollen of the Dilleniaceae clearly shows more resemblances to that of members of the Theales (or Guttiferales) than it does to ranalian families.

ACKNOWLEDGMENTS

MATERIAL EXAMINED [2]

Acrotrema bullatum Thw. CEYLON: US *1576874*.

Curatella americana L. BRAZIL: *Irwin 5470* (NY). PANAMA: *J. F. McBride 2825* (US). MEXICO: UC *1249323*. GUATEMALA: MO *1091094*.

Davilla aspera (Aubl.) Benoist. BRITISH GUIANA: *A. C. Smith 2184* (GH), HPC *1836*. TRINIDAD: *W. E. Broadway 6836* (POM). PANAMA: MO *906390*.

Davilla elliptica St. Hil. BOLIVIA: MO *1810332*.

Davilla kunthii St. Hil. COSTA RICA: *A. F. Skutch 4091* (GH), HPC *2949*. COLOMBIA: UC *963504*.

Davilla multiflora (DC.) St. Hil. MEXICO: MO *1278423*.

Davilla rugosa Poir. MEXICO: *E. Matuda 0902* (GH), HPC *2953*. PERU: MO *1082135*.

Didesmandra aspera Stapf. SARAWAK: *Burtt & Woods B.2540* (E). SARAWAK: SAR *18297*.

Doliocarpus dentatus (Aubl.) Standl. MEXICO. Yucatan: *Gentle 1418* (GH), HPC *2962*. COSTA RICA: *Skutch 3829* (GH), HPC *6271*. COLOMBIA: UC *584948*. BOLIVIA: UC *954321*. COSTA RICA: MO *1147852*.

Doliocarpus guianensis (Aubl.) Gilg. COSTA RICA: MO *1152277*.

Doliocarpus lasiogyne Benoist. BRAZIL: *Hatschbach 3580* (US). BRAZIL: UC *1088323*.

Doliocarpus major Gmel. PANAMA CANAL ZONE: *P. White 127* (GH), HPC *6272*. PANAMA: MO *1189259*; MO *1758246*. BRAZIL: MO *1255920*.

Doliocarpus olivaceus Sprague & Wms. PANAMA: Yale *11*.

Dillenia alata (DC.) Martelli. PAPUA: *Brass 7571* (A), HPC *2996*. *Hoogland 8521* (CANB).

Dillenia excelsa (Jack) Gilg. BORNEO: *Castillo 619* (A), HPC *2954*. NORTH BORNEO: *Cuadra A1019* (US). KEP *s.n.*

Dillenia indica L. AUSTRALIA: Cult. BRI *s.n.*

Dillenia luzoniensis (Vidal) Martelli ex Dur. & Jacks. PHILIPPINES: *J. P. Rojó* (CLP) *s.n.*

Dillenia megalantha Merr. PHILIPPINES: *Sulit PNH 6377* (A), HPC *2957*.

Dillenia ovata Wall. ex Hook.f. & Thoms. INDOCHINA: *Squires 775* (A), HPC *2958*. SINGAPORE: Cult. SING *s.n.*

Dillenia papuana Martelli. NEW GUINEA: *Darbyshire & Hoogland 8039* (CANB).

Dillenia parviflora Griff. THAILAND: BKF *s.n.*

Dillenia philippinensis Rolfe. PHILIPPINES: *Lambert & Brunson 39* (US); US *1861993*; *J. V. Pancho s.n.*

Dillenia reifferscheidia Villar. PHILIPPINES: *Paniza PNH 9407* (A), HPC *2960*.

Dillenia suffruticosa (Griff.) Martelli. PHILIPPINES: *Fenix 92* (GH), HPC *2961*. NORTH BORNEO: *Clemens 9504* (A), HPC *2999*. SINGAPORE: *Canright 978*; Cult. SING *s.n.*

Dillenia turbinata Finet & Gagnep. HAINAN: *Ko 52211*, HPC *1838*.

Hibbertia acicularis (Labill.) F. Muell. AUSTRALIA: *Camfield* (POM).

Hibbertia baudouinii Brongn. & Gris. NEW CALEDONIA: US *2192565*.

Hibbertia cuneiformis (Labill.) Gilg. Cult. K *s.n.*

Hibbertia dentata R.Br. Cult. K *s.n.*

Hibbertia hexandra C. T. White. NEW SOUTH WALES: *Hoogland 8585* (CANB).

Hibbertia linearis R.Br. ex DC. NEW SOUTH WALES: *Hoogland 7747* (CANB).

Hibbertia salicifolia F. Muell. NEW CALEDONIA: *Viellard 62* (A), HPC *2968*.

Hibbertia scandens (Willd.) Dryand. AUSTRALIA: *C. T. White 8237* (A), HPC *2979*. Cult. K *s.n.*

Hibbertia stellaris Endl. AUSTRALIA: *Pritzel 268* (GH), HPC *1837*.

Hibbertia stricta (DC.) R.Br. ex F. Muell. AUSTRALIA: *Giblin H19* (A), HPC *2981*.

Hibbertia tetrandra (Lindl.) Gilg. Cult. E *C3544*.

Hibbertia vestita A. Cunn. AUSTRALIA. New South Wales: *Boorman* (POM).

Pachynema junceum Benth. AUSTRALIA. Northern Territory: NT *6750*.

Pachynema dilatatum Benth. AUSTRALIA. Northern Territory: NT *6129*.

Schumacheria castaneifolia Vahl. CEYLON. Waga: *Abeywickrama s.n.*; HPC *2983*.

Tetracera alnifolia Willd. CONGO: MO *1598748*.

Tetracera arborescens Jack. BORNEO: UC *267698*.

Tetracera asiatica (Lour.) Hoogl. FORMOSA: HPC *1835*.

Tetracera boiviniana Baill. TANGANYIKA: UC *1219019*.

Tetracera euryandra Vahl. MALAYA: UC *390344*.

Tetracera fagifolia Willd. ex Schlecht. PANAMA: *I. M. Johnston 624* (A), HPC *6270*.

Tetracera indica (Houtt. ex Christm. & Panz.) Merr. SINGAPORE: *H. Keng s.n.*

Tetracera korthalsii var. subrotunda (Elm.) Hoogl. BORNEO: NY *21376*.

Tetracera macrophylla Wall. ex Hook.f. & Thoms. MALAYA: UC *243404*.

Tetracera nordtiana F. Muell. PAPUA: NY *5938*.

Tetracera ovalifolia DC. PANAMA: MO *1240100*.

Tetracera podotricha Gilg. NIGERIA: MO *1608756*.

Tetracera portobellensis Buerl. MEXICO: MO *1810305*.

Tetracera scandens (L.) Merr. PHILIPPINES: *Ahern's Coll. 104* (A), HPC *2991*. HAINAN: UC *278563*.

Tetracera volubilis L. PERU: *Schunke 168* (A), HPC *2995*. BRITISH HONDURAS: MO *1065132*.

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